

## **A Response to Landing: On Factors in the Distribution of Butterfly Color and Behavior**

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I suspect that Dr. Landing's frustration with my critique of his collected works (1985 *J. Res. Lep.* 24: 376–379) exceeds by good measure my frustration with his reply (1986 *J. Res. Lep.* 25: 67–70), but since I have been misquoted where he has quoted me, and misinterpreted by him seemingly everywhere else, a response is warranted.

Two interconnected problems pervade Landing's reply (and his original publication) which thoroughly cloud his attempts to promulgate his possibly interesting ideas. One problem is his inability to cogently couch his arguments — from a 98-word second sentence to the use of the word “parenthetically” in parentheses. The other problem is even more exasperating. Landing refuses to play by the “rules” of scientific inquiry. In his reply, he buries errors of interpretation under the same muddled reasoning I complained of in his book. Therefore, I limit myself here to just a couple of points in that reply.

Landing states that I “object to the use of models” and that my definition of ecological niche “is inadequate for butterflies.” I do not object to the use of models; what I argued was that his construct does not function as a model. It does not predict, does not simplify nature, and does not shed light on processes.

Regarding ecological niche, I noted that the term has a formal definition, in use since it was proposed by Hutchinson more than forty years ago. If the term is “inadequate,” that is, does not describe the situation, then Landing should not use the term. By creating his own definition for the term and by not telling his readers, Landing simply confuses. If he feels the vertical sorting of butterflies by color is a key factor in the structuring of butterfly communities, then a term for that does exist. Factors acting on “each stage of the life cycle” are called niche components. The sum of individual niche components (perhaps, such as the vertical position of a certain butterfly species) make up the niche of a given species. Gilbert and Singer (1975, *Ann. Rev. Ecol. Syst.* 6: 365–397, following Owen 1959, *Entomol. Gaz.* 10: 27–38), for instance, define key niche components of butterflies as (1) larval food plants, (2) parts of host used, (3) times of appearance (phenology and voltinism), (4) habitats, (5) adult resources, and (6) parasite and predator escape. They note that these niche components interact in complex ways, and might have noted that each of these niche components could be subdivided and

that other equally important components well might exist. Each individual niche component must be understood in order to understand the behavior of individual butterflies, the dynamics of their populations, and, ultimately, the structure of butterfly communities. Landing certainly presents no evidence in his treatment that "butterfly color" alone is the niche component which explains the structuring of communities.

Landing seems not to be particularly well-versed in butterfly biology in general. Many of his observations on mimicry were made by previous authors long ago. His statements on the "heat collecting capacity of different wing colors" are especially naive. Clench (1966, *Ecology* 47: 1021–1034) notwithstanding, butterfly wings are not radiators for hemolymph (e.g. see Watt 1968, *Evolution* 22: 437–458 and Kingsolver's review, *J. Res. Lep.* 24: 1–20, for a discussion of the role of wing color in thermoregulation). He, additionally, says that he does not see how nectar as a limiting resource could play a role in the distribution of butterfly "color types." Yet, all factors acting on the distribution of butterflies affect the frequencies of "color types" in specific habitats. Nectar resources can dramatically affect habitat suitability and population structure, and thereby the distribution of butterflies of certain colors in their physical environments, even for temperate zone butterflies which are thought to be relative generalists in their selection of adult food sources (Gilbert and Singer 1973, *Amer. Nat.* 107: 58–73; Murphy 1983, *Environ. Ent.* 12: 463–466; and Murphy et al. 1984, *Oecologia* 62: 269–271).

Finally, there is Landing's dumbfounding assertion that the discussion of Papageorgis's work (1975, *Amer. Sci.* 63: 522–532) in a general text somehow renders as facts the conclusions she drew in her original work. May I suggest that it is a fact that certain species tend to fly in certain places. That community structure of heliconiines and ithomiines is largely determined by the co-occurrence of species sharing certain color patterns is a falsifiable hypothesis, hence subject to testing. That selection has "geared color pattern to height of flight in the vegetation because each pattern is most effectively cryptic at that level," is speculation which probably is not falsifiable. How would one develop an adequate test of that in the field?

In conclusion, I certainly hope that Dr. Landing withholds his promised 300 page manuscript-to-be until he can offer something more than circular reasoning and unsupported supposition in the guise of biological data. Then again, I do sort of look forward to an explanation of what Landing calls "intra-individual Muellierian mimicry." Landing doesn't consider that a "radical idea." I certainly do.